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CROSSING THE ULTIMATE ECOLOGICAL BARRIER: EVIDENCE FOR AN 11 000-KM-LONG NONSTOP FLIGHT FROM ALASKA TO NEW ZEALAND AND EASTERN AUSTRALIA BY BAR-TAILED GODWITS

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Abstract. Populations of the Bar-tailed Godwit (*Limosa lapponica*; Scolopacidae) embark on some of the longest migrations known among birds. The *baueri* race breeds in western Alaska and spends the nonbreeding season a hemisphere away in New Zealand and eastern Australia; the *menzbieri* race breeds in Siberia and migrates to western and northern Australia. Although the Siberian birds are known to follow the coast of Asia during both migrations, the southern pathway followed by the Alaska breeders has remained unknown. Two questions have particular ecological importance: (1) do Alaska godwits migrate directly across the Pacific, a distance of 11 000 km? and (2) are they capable of doing this in a single flight without stopping to rest or refuel? We explored six lines of evidence to answer these questions. The distribution of resightings of marked birds of the *baueri* and *menzbieri* races was significantly different between northward and southward flights with virtually no marked *baueri* resighted along the Asian mainland during southward migration. The timing of southward migration of the two races further indicates the absence of a coastal Asia route by *baueri* with peak passage of godwits in general occurring there a month prior to the departure of most birds from Alaska. The use of a direct route across the Pacific is also supported by significantly more records of godwits reported from within a direct migration corridor than elsewhere in Oceania, and during the September to November period than at other times of the year. The annual but rare occurrence of Hudsonian Godwits (*L. haemastica*) in New Zealand and the absence of their records along the Asian mainland also support a direct flight and are best explained by Hudsonian Godwits accompanying Bar-tailed Godwits from known communal staging areas in Alaska. Flight simulation models, extreme fat loads, and the apparent evolution of a wind-selected migration from Alaska further support a direct, nonstop flight.

Key words: Bar-tailed Godwit, energetics, flight mechanics, Limosa lapponica, *migration, Oceania, wind-selected migration.*

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Atravesando la Barrera Ecológica Final: Evidencia de un Vuelo sin Escala de 11 000 km de Longitud desde Alaska a Nueva Zelanda y el Este de Australia por *Limosa lapponica*

Resumen. Las poblaciones de *Limosa lapponica* (Scolopacidae) se embarcan en una de las migraciones más largas conocidas para aves. La raza *baueri* cría en el oeste de Alaska y pasa la estación no reproductiva a un hemisferio de distancia en Nueva Zelanda y el este de Australia; la raza *menzbieri* cría en Siberia y migra hacia el oeste y el norte de Australia. Aunque se sabe que las aves de Siberia siguen la costa de Asia durante ambas migraciones, la ruta meridional que siguen las aves reproductivas de Alaska ha permanecido desconocida. Dos preguntas tienen particular importancia ecológica: (1) ¿las aves de Alaska migran directamente a través de Pacífico, a lo largo de 11 000 km? y (2) ¿son capaces de hacerlo en un único vuelo sin parar a descansar y reabastecerse? Exploramos seis líneas de evidencia para responder a estas preguntas. La distribución de avistamientos de aves marcadas de las razas *baueri* y *menzbieri* fue significativamente diferente entre vuelos hacia el norte y el sur, sin que hubiera prácticamente un solo avistamiento de individuos marcados de *baueri* a lo largo del continente asiático durante la migración hacia el sur. El período de la migración hacia el sur de ambas razas indica la ausencia de una ruta costera asiática para *baueri*, con un pico en el paso de las aves ocurriendo allí un mes antes de la partida de la mayoría de las aves desde Alaska. El uso de una ruta directa a través del Pacífico también está avalado por un número significativamente mayor de aves reportadas para un corredor migratorio directo que para cualquier otro lugar de Oceanía, y para el período entre septiembre y noviembre que para otros momentos del año. La presencia anual, aunque rara, de *L. haemastica* en Nueva Zelanda y la ausencia de registros a lo largo del continente asiático también avalan la posibilidad de un vuelo directo y se explican mejor por el hecho de que *L. haemastica* acompaña a *L. lapponica* desde áreas de escala comunes en Alaska. Evidencia complementaria de un vuelo directo sin escalas está dada por modelos de simulación de vuelo, la gran acumulación de grasa en las aves y la aparente evolución de una migración seleccionada por el viento.

INTRODUCTION

The timing of human settlement of the Earth's biomes appears to be related not only to the physical extent of ecological barriers encountered but also to the inhospitable nature of the barriers. In this sense, the Pacific Ocean arguably represents the most formidable ecological barrier, with human expansion into the far reaches of Oceania occurring only within the past 3000–4000 years (Hurles et al. 2003). But does the Pacific present a similar ecological barrier to birds? Obviously not to those forms adapted for existence on and from the sea. And surprisingly not for many terrestrial birds, as more such species have migrations crossing portions of the Pacific than across any other ocean (Williams and Williams 1999). For example, several species of shorebirds migrating from Alaska must cross a minimum of 3500 km of open ocean before reaching Hawaii and even large portions of these populations overfly the Hawaiian Archipelago en route to the next available land 3000 km farther south (Thompson 1973, Williams and Williams 1988, 1990, 1999, Marks and Redmond 1994, Johnson 2003). The limits of such nonstop flights are pushed even further by Red Knots (*Calidris canutus*) and Bar-tailed Godwits (*Limosa lapponica*), which migrate northward from southeastern Australia and New Zealand to staging sites along the coast of the Yellow Sea, a distance of over 8000 km (Battley 1997, Battley and Piersma 2005, J. Wilson and C. Minton, unpubl. data).

Two recognized subspecies of Bar-tailed Godwit occur in the central Pacific basin (Higgins and Davies 1996, Engelmoer and Roselaar 1998, McCaffery and Gill 2001). The *L. l. menzbieri* population breeds in central northern Siberia from the Yana River delta east to Chaun Gulf and spends the nonbreeding season in western and northern Australia. Members of the *L. l. baueri* population nest in western and northern Alaska and spend the nonbreeding season in New Zealand and eastern Australia. (In the Anadyr Basin area of Chukotka is a third, much smaller breeding population of unresolved taxonomic affinity and nonbreeding area [Engelmoer and Roselaar 1998, McCaffery and Gill 2001].) The *menzbieri* population, numbering about 170 000 birds, appears to migrate both north and south in a two-stage flight with the main northward leg from western Australia to the Yellow Sea and Korean Peninsula entailing a 6000-km-long nonstop effort (Barter and Wang 1990, Wilson and Barter 1998), and the main southward leg a 6000- to 8000-km-long

flight from the Sea of Okhotsk or Yellow Sea regions to northwest Australia (M. Barter, pers. comm.). The *baueri* population is slightly smaller (Driscoll 1997, Gill and McCaffery 1999, McCaffery and Gill 2001) and during northward migration birds are thought to undertake a single flight of between 5000 and 8000 km from New Zealand and eastern Australia to the Korean Peninsula, Japan, and the north coast of the Yellow Sea (Riegen 1999, Battley and Piersma 2005, J. Wilson and C. Minton, unpubl. data). Intensive marking programs initiated in New Zealand and Australia in the late 1970s (Riegen 1999, Minton 2004) have shown that birds marked within the nonbreeding range of *baueri* do not occur along the Asian coast during southward migration. This finding led Barter (1989) and others (Barter and Wang 1990, Riegen 1999, J. Wilson and C. Minton, unpubl. data) to speculate that the southward flight is instead direct across the Pacific, a minimum distance of about 9700 km to northeastern Australia and 10 800 km to New Zealand.

Mäori folklore lends support to godwits crossing this large ecological barrier. When living on a small Pacific island north of New Zealand they noticed that the küaka (Bar-tailed Godwit) migrated every year in a southerly direction. From this evidence they deduced that land was to be found to the south and canoes were outfitted for a voyage that eventually led to the discovery of Aotearoa (New Zealand), their new home (Gudgeon 1903, Te Paa 1912, Phillipps 1966, Riley 2001).

Building upon these millennia-old observations, our objective here was to answer two fundamental and oft-pondered questions concerning the southward migration of the *baueri* race of Bar-tailed Godwit: (1) do birds migrate across the Pacific Ocean between Alaska and New Zealand, a distance of 11 000 km? and (2) are they capable of doing this in a single flight without stopping to rest or refuel? We addressed these questions by exploring six lines of evidence: (1) distributional records and chronology of occurrence of godwits during migration periods, (2) differential resighting rates of leg-flagged birds during northward and southward migrations, (3) comparisons between departure and arrival events recorded at migration termini, (4) annual occurrence of a congener, the Hudsonian Godwit (*L. haemastica*), in Oceania, (5) analyses of maximum flight ranges, and (6) synoptic weather and wind-field analyses across the Pacific and atmospheric trajectory models at time of known departure events.

METHODS

DISTRIBUTIONAL RECORDS AND CHRONOLOGY THROUGHOUT OCEANIA

If godwits undertake a direct transpacific flight from Alaska to New Zealand and eastern Australia they would be expected to occur in central Oceania either as occasional fallouts from migrating flocks or at regularly used stopover sites. To assess this, we turned to various sources, including Byrne (1979), Heather and Sheehan (1990), references in serial publications such as *Atoll Research Bulletin*, *Sea Swallow*, and *Birds of North America* (McCaffery and Gill 2001, Gill et al. 2002, Marks et al. 2002), and unpublished databases maintained by R. Pyle, P. Donaldson, and D. Watling. We also referenced the extensive collections of birds and field notes from the Whitney South Seas Expedition and the Pacific Ocean Biological Survey Program (maintained at the American Museum of Natural History and the U. S. National Museum, respectively) and we searched ornithological collections of major museums (Australia Museum, Bernice Bishop Museum, Honolulu; Field Museum of Natural History, Chicago; and Museum of Vertebrate Zoology, Berkeley). Combined, the above sources represent over 300 field assessments (many with multiple records) collected since the early 1920s. Admittedly, such distributional records may present a somewhat biased portrayal of the spatial and temporal occurrence of birds because field efforts were not distributed evenly across the region or season. Many studies reported when godwits were encountered but did not provide the range of dates when investigators were present but no godwits were observed. Because of these potential biases, we used these records to provide a general pattern of monthly occurrence throughout the region. Thus, the 568 'monthly records' represent the presence of one or more investigators at a particular site for one or more days in a given month during which the presence or absence of Bar-tailed Godwits was noted.

We also assessed seasonal occurrence from census data obtained at two sites (both in Fiji; but see Stinson et al. 1997 for the Mariana Islands) where counts have been conducted throughout the annual cycle (Skinner 1983, D.

Watling, unpubl. data). For Skinner (1983) we used high monthly counts and for Watling, whose biweekly counts spanned a longer period, we present an average of all counts within a given month.

Throughout this paper we define Oceania to include all insular bodies in the north-central to south Pacific Ocean, including those in Micronesia, Melanesia (but not the main island of New Guinea), Polynesia, and the Hawaii Archipelago, but excluding New Zealand proper, Australia, and Indonesia (after Bier 1995).

BAND RECOVERIES AND SIGHTINGS OF LEG-FLAGGED BIRDS

Since the early 1980s, about 10 000 godwits have been marked with various colors of leg flags specific to individual countries or regions—primarily in Australia and New Zealand, but also in China, Japan, and the Republic of Korea (see Acknowledgments). Almost annually since the mid-1990s there have been efforts dedicated to observing these marked birds, both on the migration-staging grounds in Alaska (e.g., Gill and McCaffery 1999) and at migration-stopover sites along the coast of Asia (Minton et al. 2002). For this effort we relied heavily on previous summaries of these recovery and resighting data (Riegen 1999, Minton et al. 2002, J. Wilson and C. Minton, unpubl. data).

TIMING OF ARRIVAL AND DEPARTURE

To assess levels of concordance between periods of departure and arrival, we relied on available seasonal census data from breeding, nonbreeding, and migratory stopover sites of both the *baueri* and *menzbieri* subspecies. Most of these studies were conducted independently of each other and focused on site-specific issues and not broad geographic regions or range-wide assessments. Nevertheless, they are of sufficient number and scope that comparisons can be made, especially within the past decade, when we made concerted efforts to document departures from Alaska and arrivals in New Zealand.

MAXIMUM FLIGHT RANGE PREDICTIONS

For an energy-based evaluation of the proposed 11 000-km-long transpacific flight by godwits we computed maximum flight range—i.e., the distance flown until the fuel store was depleted—under various conditions using Program FLIGHT 1.15 (Pennycuick 2004). This advanced program encompasses a family of flight-mechanic models that account for use of protein stores during long-distance flights (Pennycuick 1989, 1998). Use of this program to derive flight ranges was greatly enhanced through recent validation of its performance by Pennycuick and Battley (2003), who looked at the 5400 km-long-flight of the Great Knot (*Calidris tenuirostris*), another long-distance migrant scolopacid wader. Using a set of realistic assumptions and empirical data on body mass and composition obtained from birds collected at both the start (Northwest Australia) and end (China) of the flight (see Battley et al. 2000), they were able to estimate correctly fat used during flight and body mass on arrival.

The variables we used in program FLIGHT and their settings are presented in Table 1. The general assumptions for the various parameters are justified in the explanatory notes that accompany the program (based on Pennycuick 1989, 1998) or appear in Pennycuick and Battley (2003). However, we also make several specific assumptions. Primarily for comparison with other studies, we have assumed that birds fly at sea level, but we also ran simulations at 1500-m altitude. Choice of flight height has only a very minor effect on the predicted maximum flight range because flying higher—with lower air densities, higher flight speeds, and shorter flight times—comes at the expense of higher values for specific work, specific power, and greater demands on the respiratory and circulatory systems (Pennycuick and Battley 2003). We followed Pennycuick and Battley (2003) when considering flight speed and, instead of using a calculated maximum range speed (V_{mr}), we set air speed at 1.2 times the minimum power speed (V_{mp}) at the beginning of the flight and held it constant throughout the flight. We did this because as body mass declines, the (robust) estimate of V_{mp} also declines, leading to an increase in the ratio between V and V_{mp} (Pennycuick and Battley 2003). Although this leads to a small reduction of flight range, flight at constant speed would also lead to what Pennycuick and Battley (2003) called ''an avoidance of unduly high power requirements'' when the birds are fully loaded at the start of the migration. For body drag coefficients we considered two values, one of 0.1 (from Pennycuick and Battley 2003) and a lower value (0.05) suggested by Pennycuick et

TABLE 1. Variables used in the simulation of maximum flight ranges (distance to depletion of fuel store) for male Bar-tailed Godwits departing Alaska on an 11 000-km-long flight[a] to New Zealand and eastern Australia (Program FLIGHT, version 1.15).

Variables (SI-units)	Values
General assumptions[b]	
Basal metabolic rate equation[c]	for non-passerines
Induced power factor	1.2
Profile power ratio	0.903
Acceleration due to gravity (m sec^{-1})	9.81
Fat energy density (J kg^{-1})	3.90×10^7
Dry protein density (J kg^{-1})	1.83×10^7
Protein hydration ratio[d]	2.2
Conservation efficiency	0.23
Circulation and respiration factor	1.1
Density of muscle (kg m^{-3})	1060
Mitochondria inverse power density (m^3 W^{-1})	1.2×10^{-6}
Power density of mitochondria	constant
Specific assumptions[e]	
Altitude of flight (m)	0 or 1500
Air density (kg m^{-3})	1.23
Starting ratio V:V_{mp}	1.2
Flight speed during trip[f]	constant
Specific work	constant
Minimum energy from protein (%)	5
Body drag coefficient	0.1 or 0.05
Bird-related measurements	
Wing span (m)[g]	0.73
Aspect ratio[h]	9.3
Wing area (m^2)[i]	0.0573
Body mass at start (g)[j]	455, 485, or 515
Fresh mass of pectoral muscle at start (g)[j]	67, 72, or 76
Fat mass at start (g)[j]	always 200
Airframe mass at start (g)[j]	188, 213, 239

[a] The great circle distance between the most northerly Alaska staging site (Yukon Delta) and the northern tip of New Zealand is 10 700 km; that between the most southerly staging site (Nelson Lagoon) and northern Queensland, Australia, is 9700 km. We assume godwits follow a great circle route (orthodrome), though a constant compass course (loxodrome route) would likely add little additional distance since the departure and arrival sites occur along a north-south axis.

[b] Based on standard settings in the program FLIGHT and as verified by Pennycuick and Battley (2003).

[c] Changing it to the passerine equation in view of the high values of BMR in many shorebirds (Kersten and Piersma 1987) has remarkably little effect on the model outcomes (see program FLIGHT).

[d] This is the ratio of water released and lost through respiration as dry protein is combusted, assuming that water makes up 69% of wet protein.

[e] Specific to southward migrating *baueri* godwits, with the body drag coefficient and altitude being varied.

[f] Flight speed (i.e., true air speed; see program FLIGHT) is a function of the starting body mass.

[g] Based on a sample of 26 male *baueri* godwits from nonbreeding grounds in New Zealand (Battley and Piersma 2005).

[h] Based on a sample of wing tracings of three *baueri* godwits from Alaska (C. J. Pennycuick, pers. comm.).

[i] Computed from wing span and aspect ratio.

[j] Based on a variety of body mass and composition values.

al. (1996) as being more pertinent to birds with highly streamlined bodies, such as shorebirds.

Lastly, we also made an important assumption regarding types of fuel burned. If specific work of the muscles is constant, then, with the lowering of body mass in the course of the flight, we assumed that excess muscle would be oxidized as fuel, reducing the amounts that needed to be taken from the fat store. Given the evidence that birds actually *need* to consume protein during long distance flights (Jenni and Jenni-Eiermann 1998, Battley et al. 2001, Jenni-Eiermann et al. 2002), and that they may take this protein from organs other than the pectoral

muscles (Battley et al. 2000), we assumed that a minimum of 5% of the energy demand was based on the burning of protein. If the pectoral muscles did not supply enough protein, the remainder was taken from the 'airframe mass,' the 'structural' fat-free mass of the body.

For bird-related measurements required of the program we restricted our analysis to fully-grown adult males. (The performance values for females were very similar to those of males and are thus not presented.) The most critical linear dimension is wingspan, for which we use measurements of 26 adult male *baueri* godwits collected in New Zealand (Battley and Piersma 2005). For aspect ratio we used a value of 9.3 based on wing tracings of males and females from the same New Zealand sample (C. J. Pennycuick, pers. comm.); note that the predicted flight ranges are not very sensitive to wing span values that do not deviate more than 0.05 m. Adult male body mass at departure from Alaska was based on the masses of two birds (Alaska Science Center specimen nos. 0051, 0052) with maximum visual fat scores, each weighing 485 g, collected on 20 September 1976 at Nelson Lagoon, Alaska Peninsula (R. E. Gill, unpubl. data). These weights are at the high end of the range for adult males collected during fall stopover (McCaffery and Gill 2001) and close to the average of 503 g in the adult males collected before northward departure from New Zealand (Battley and Piersma 2005). These New Zealand birds contained an average of 190.5 ± 21.3 g of fat. Nine juveniles killed upon collision with a radar dome on the Alaska Peninsula in mid-October 1987 (probably embarking on a transpacific flight) contained an average of 201.4 ± 20.4 g of fat (Piersma and Gill 1998). These juveniles were not fully grown with respect to skeleton and integument (P. Battley and T. Piersma, unpubl. data), thus their body size measurements cannot be used in the program FLIGHT (contra Pennycuick and Battley 2003). Based on the fat levels in the New Zealand males and the Alaska Peninsula juveniles, we considered a fat load of 200 g to be a realistic value for adult males starting their journey from Alaska. Lastly, given the high correlation between pectoral muscle mass and body mass in Bar-tailed Godwits worldwide (Piersma and Gill 1998), we considered pectoral mass 0.148 of body mass at the start of the journey based on data for juvenile males used in Piersma and Gill (1998). Subtraction of fat and pectoral muscle mass from body mass led to the starting value for the airframe mass.

Program FLIGHT uses a 'time-marching' routine. Beginning with starting values it assumes that all measurements stay constant over a 6-min interval and then it calculates how much fat and protein are consumed in order to yield starting values for body mass, wing-beat frequency, flight speed, power, and a number of other variables needed to begin the subsequent 6-min interval. It repeats this procedure until all fat is used up and then lists the total time spent in flight, body mass and composition at arrival, distance flown, etc. Using FLIGHT, we focused on the effects of a 60-g range in body mass centered on a starting mass of 485 g while keeping fat mass constant at 200 g. We followed this procedure since we were particularly interested in examining the question of whether the protein stores left before departure (see Piersma and Gill 1998, Piersma et al. 1999) might actually limit flight range. We also briefly explored the effects of (1) differences in pectoral muscle mass on flight range while keeping body mass at start constant, and (2) differences in fat mass while keeping lean mass constant. Of particular relevance in this evaluation were the predicted arrival mass and the predicted size of the pectoral muscles still remaining when the 'virtual godwits' ran out of fat. The range in body masses found in male Bar-tailed Godwits captured upon their arrival in October in New Zealand (in Higgins and Davies 1996, Miskelly et al. 2001) suggests that simulations with assumptions that lead to predicted arrival masses lower than 210–225 g cannot be accepted.

ENVIRONMENTAL DATA

In the previous simulations we assumed flight speed was unaffected by winds, but a number of waterbird species staging in southwest Alaska have been shown to have wind-aided southward migrations. To learn if departures of godwits from Alaska were correlated with weather, we looked at synoptic weather and wind-field data from the September–November migration period. From this we wanted to learn not only what weather characteristics were associated with known departure events but also the frequency, intensity, and tracks of storms that occurred throughout the North Pacific during the staging period. This in turn prompted us to look at en route winds, both those associated with depar-

tures and those across the central and southern Pacific Ocean. A thorough analysis of en route winds is beyond the scope of this paper, but use of state-of-the-art global wind models in conjunction with documented departure events could reveal large-scale wind-field patterns throughout the course of the documented migrations. To learn the extent of favorable winds provided by storms during departure we used a Lagrangian atmospheric trajectory model (CMC 2001). The model uses three-dimensional wind fields to estimate the origin or destination of an air 'parcel' from a specific location in space and time. We used diagnostic wind fields at 6-hr intervals (from Global Data Assimilation System archives of the Canadian Meteorological Centre [CMC]) and trajectories at various heights (from near surface to 2000 m) from sites with observed departures during model runs.

To assess winds over the Pacific Ocean once birds departed on migration we used two sources. For the observed departure in 1987 we obtained data from the NOAA-CRIES Climate Diagnostic Center (CDC 2004); for all other departures we used data from the CMC Global Data Assimilation and Forecast System (CMC 2004). For this effort both have been converted to a $10^\circ \times 10^\circ$ grid. Even though it is unlikely that birds migrate at a constant altitude, we simplified our analysis by selecting winds at the 850 mb ($\sim$1500 m) level, a general height at which shorebirds in other studies have been shown to migrate (citations in Green 2003). To develop composite snapshots of winds en route for each of the four observed departures we assumed the flight required about six days. We then looked at winds at 24-hr intervals (beginning with departure) within three of the wind regimes across the Pacific: (1) polar easterlies and north-temperate westerlies ($\sim$60–30°N); (2) equatorial trades and doldrums (30°N–10°S); and (3) southern hemisphere westerlies (10–40°S). Lastly, we realize that godwits likely adjust air speed to wind conditions en route and that transit time through wind regimes might vary by several hours, especially at the start and end of the flight where winds are typically much more dynamic compared to the middle, equatorial portion where winds are generally benign. Because of this, our graphic presentation of en route winds is based on differing time periods within three regions of latitude that span the projected flight corridor. Winds depicted during the initial stage of the flight are at departure but also generally representative of conditions during the ensuing 48-hr period; those through the middle latitudes depict the subsequent 60-hr period; and those in the south represent the conditions upon arrival and over the preceding 36 hr.

STATISTICAL ANALYSES

To look specifically at the occurrence of godwits in Oceania during southward migration, we first had to define the migration period and the likely pathway followed by birds. We considered the migration period to encompass the earliest departure from Alaska (early September) and the peak arrival in New Zealand (into early November). For a likely migration corridor we assumed birds generally follow a great circle route between the staging grounds in Alaska and the nonbreeding grounds in Australia and New Zealand, with the outer bounds of the corridor inscribed by great circle arcs that link the east and west extents of the respective ranges. We then plotted records of presence or absence of godwits during the September–November period and used a chi-square goodness-of-fit test to compare the proportions occurring within and outside of the transpacific migration corridor. We also used a chi-square test to compare the proportion of birds (maximum counts) occurring inside and outside the migration corridor. Birds were considered to use a site if they had ever been recorded there; these included sites surveyed during multiple years but for which birds were not reported in some years. For numeric comparisons of birds inside and outside the proposed migration corridor, we took a conservative approach and assumed that some proportion of birds recorded at a particular site during southward migration remained there for extended periods (see McCaffery and Gill 2001, D. Watling, pers. comm.) and may have been included in counts spanning two or more consecutive months. Thus, to mitigate possible issues of pseudoreplication, we used the single highest of the monthly maximum counts from sites at which two or more months were reported. We then compared the average maximum count inside and outside the migration corridor using a Mann-Whitney *U*-test. Differences in seasonal and regional resighting rates of leg-flagged birds were assessed using chi-square tests. The distribution of resightings in Asia, however, is biased geographically in that most effort to date has

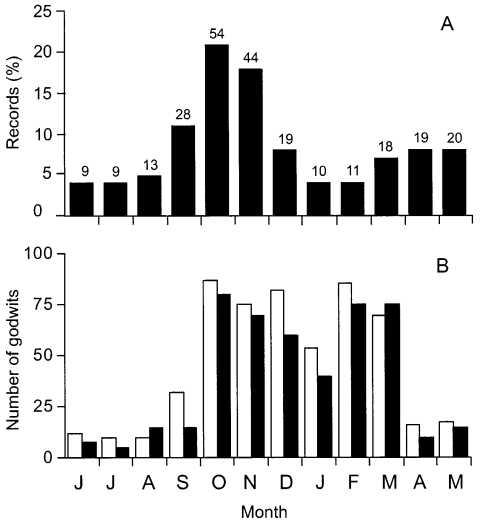


FIGURE 1. (A) Percentage of total records of occurrence (n = 254) of Bar-tailed Godwits throughout Oceania each month. Numbers above bars show number of records. (B) Number of godwits recorded during monthly censuses at Suva Point, Fiji; solid bars from Skinner (1983) and open bars from D. Watling (unpubl. data).

occurred in Japan and Republic of Korea and larger areas like the Yellow Sea and Sea of Okhotsk have received comparatively little coverage, especially during the southward migration period. Despite this shortcoming, coverage has been adequate to establish seasonal patterns over broad regions. Data are reported as means ± SD.

RESULTS

SEASONAL OCCURRENCE, DISTRIBUTION, AND NUMBERS OF BIRDS IN OCEANIA

We found records of godwits in Oceania during every month of the year (Fig. 1A), but most frequently during the southward migration period (September–November), which comprised 49% of all monthly records (n = 254). No other month accounted for more than 8% of the total. We found a similar temporal pattern at Suva Pt., Fiji, the only site in Oceania at which systematic counts of godwits have been conducted for extended periods (Fig. 1B).

The geographic occurrence of godwits in Oceania was widespread, with birds noted from most (77%) of the 30 major archipelagoes and from over 350 different atolls and islands within. Only from central and eastern Polynesia (e.g., Southern Cook, Marquises, Austral, Gambier, Line, most of the Tuamotu, and Pitcairn islands) have birds not been recorded.

We also found a significant difference between the southward migration period and the rest of the year (χ^2_1 = 32.4, $P < 0.001$) when we looked at geographic distribution of records in Oceania by season. Most sites where godwits were recorded during the September–November period occurred throughout a corridor linking Alaska and the nonbreeding grounds in eastern Australia and New Zealand (Fig. 2). The same pattern was found when total maximum counts per site were compared inside and outside the migration corridor. When adjusted for sites with multi-year records, 93% (n = 868) of all godwits noted during the southward migration period came from sites within the likely migration corridor. The proportion increased to 97% when records just outside but east of the corridor (Hawaiian and Cook islands) were also considered (Fig. 2). Most (87%) of the 868 birds were recorded from four sites in the southern half of the migration corridor: Mankin Atoll (120 birds) in the Tungaru Islands, Rewa River (200 birds) and Suva Point, Fiji (121 birds), and Chatham Island (314 birds) east of New Zealand (Fig. 2). When these four sites are not considered, the average maximum number of godwits recorded at sites elsewhere in Oceania during southward migration was similar both outside (4.6 ± 7.1, range 1–21) and inside (2.8 ± 3.9, range 1–20) the corridor (Mann-Whitney U-test: z = 0.9, n = 13, 37, P = 0.19).

RESIGHTINGS OF MARKED BIRDS

The proportions of color-flagged godwits of the two subspecies that were resighted along the coast of Asia during northward and southward migrations differed markedly (Table 2; χ^2_1 = 36.8, $P < 0.001$). On northward migration both *baueri* and *menzbieri* regularly used intermediate stopover sites; during southward migration, however, *menzbieri* were still commonly sighted along the coast of Asia whereas *baueri*—with but three exceptions—have gone unreported. Sightings of marked *baueri* (n = 136; R. Gill and B. McCaffery, unpubl. data)—but not of marked *menzbieri*—on the Alaska staging grounds from late August through September (1999–2004) further indicate the extent of separation of the two subspecies during southward migration.

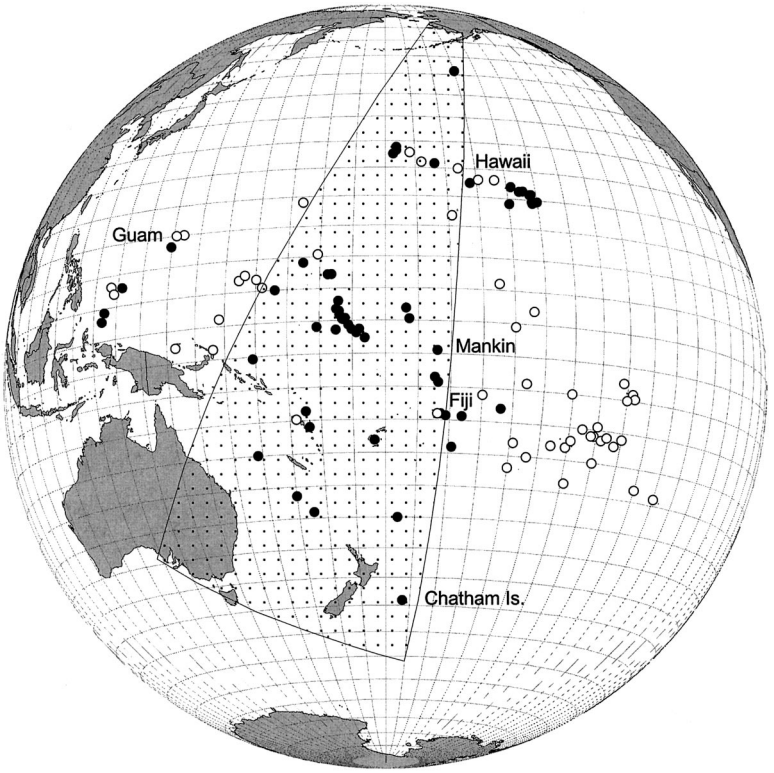


FIGURE 2. Distribution of records of Bar-tailed Godwits throughout Oceania during the southward migration period (September–November). Filled circles = sites reporting godwits; unfilled circles = sites at which no godwits were noted during the period. Map projection = Orthographic (central meridian = 180; reference latitude = −10). Lateral bounds of stippled region = plotted great circle routes.

TIMING OF DEPARTURE AND ARRIVAL

The average peak departure of godwits from Alaska and peak arrival in Fiji, New Zealand, and eastern Australia occur within a 2- to 3-week period in late September through mid-October (Fig. 3). Both departure from Alaska and arrival in New Zealand can be earlier, however, as recorded in 2003 when birds were seen leav-

TABLE 2. Seasonal distribution of resightings and recoveries of *baueri* and *menzbieri* subspecies of Bar-tailed Godwits along the coast of East Asia during northward and southward migration. All putative *baueri* were marked on nonbreeding grounds in New Zealand and eastern Australia; *menzbieri* were marked in western Australia (but see footnotes for few exceptions). See methods section for details on the sources of data.

Location observed	Northward		Southward	
	baueri	*menzbieri*	*baueri*	*menzbieri*
Russia	2	3	2	5
Japan	84[a]	1		2
North Yellow Sea	18	38	1	2
Republic of Korea	62	54		35
Hong Kong, Taiwan, SE China[b]	2	52		1
Total	168	148	3	45

[a] Includes one bird flagged in Japan in August and seen in New South Wales, Australia, the following February.
[b] Includes 40 birds (1 *baueri* and 39 *menzbieri*) shot by hunters; remainder are resightings of flagged birds including one juvenile flagged in Hong Kong and recovered in northwest Australia.

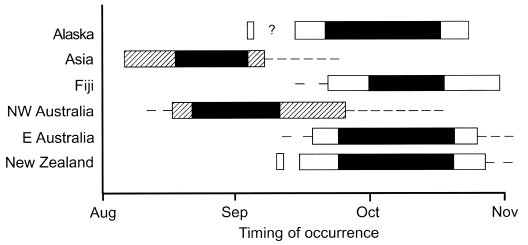


FIGURE 3. Timing of southern migration of Bar-tailed Godwit races *baueri* (unfilled bars) and *menzbieri* (cross-hatched bars) at different locations along their migration routes. Filled portions of bars indicate periods of peak passage; dashed lines indicate periods of movement. Information for Alaska from Gill and McCaffery (1999), McCaffery and Gill (2001), R. Gill, unpubl data; for Asia, Moores (1999), Satoshi (2003); for Fiji, Smart (1971), Skinner (1983), D. Watling, unpubl. data; for NW Australia, Higgins and Davies (1996), J. Wilson and C. Minton, unpubl. data, D. Rogers and M. Barter, in litt.; for SE Australia, Higgins and Davies (1996), Keates (2003), M. Barter, pers. comm.; for New Zealand, Hawkins (1980), Sagar et al. (1999), Riegen (1999), A. Riegen, unpubl. data.

ing during the first week of September (Table 3) and first arrivals were noted in New Zealand 6–10 days later (A. Riegen and P. Battley, unpubl. data). In contrast, southward passage of *menzbieri* godwits along the coast of Asia and arrival in Western Australia are a month earlier and essentially over before most *baueri* godwits depart Alaska (Fig. 3).

MAXIMUM FLIGHT RANGE PREDICTIONS

With a starting body mass of 485 g, a fat mass of 200 g (41% body fat), and pectoral muscles adjusted to body mass, male Bar-tailed Godwits would be able to cover 11 000 km under still air conditions only if their body drag coefficient was as low as 0.05 (Table 4, Fig. 4). Under either assumption for body drag, arrival body mass (213–214 g, or 75% of the lean mass at start) would be reasonable. (Note that Battley et al. [2000] found lean mass of Great Knots that arrived after a 5400 km long flight to be ca. 80% of lean mass at departure.) Pectoral muscle masses of godwits at arrival (21–33 g) were small, but not unrealistically so (Landys-Ciannelli et al. 2003). A body drag coefficient of 0.05 appears to be realistic for godwits since it produces a more consistent prediction of air speed (18.6 m sec^{-1}, or 67 km hr^{-1}), i.e., a value that is much closer to empirical values obtained by radar for godwits of the *L. l. taymyrensis* subspecies dur-

TABLE 3. Conditions during departures of Bar-tailed Godwits on southward migration from sites on the Alaska Peninsula.

		Storm characteristics			Departure site winds		Tailwind component[d]		
Departure period[a]	Number of birds (number of flocks)[b]	Low center position	Pressure (mb)	Distance & direction[c] from departure point	Speed ($m\ sec^{-1}$)	Direction	Speed ($m\ sec^{-1}$)	Direction	Fetch (km)[e]
20 Oct 1987 (09:30)	>9 (?)	47°N, 174°W	976	1100 km; 225°	10	N	10–21	NNW-NW	1200
24 Sep 1996 (03:00–07:00)	492 (1)	43°N, 175°W	974	1650 km; 237°	4–8	NNE	8–23	N-NW	1300
10–11 Oct 2000 (04:00–20:00)	>4000 (?)	55°N, 160°W	986	650 km; 184°	5–10	NNE	13–23	N-NW	900
3–5 Sep 2003 (09:00–10:00)	5090 (15)	47°N, 162°W	998	900 km; 183°	0–5	N	8–15	N-NNW	1100

[a] 1987 departure point: Cold Bay (55°20′N, 162°50′W); 1996 and 2000: Nelson Lagoon (56°00′N, 161°00′W); 2003: Egegik Bay (58°10′N, 157°30′W). All times Coordinated Universal Time (add 10 hr for local, Alaska Daylight Time).

[b] For details of 1987 departure see Piersma and Gill (1998); 1996 observation by R. Gill and M. Owens; 2000 observation by R. Gill; 2003 observation by R. Gill and D. Ruthrauff.

[c] Direction relative to true north from departure site.

[d] Winds along likely initial migration route from departure site.

[e] Fetch is the longest distance with sustained winds from tail or quartering tail direction.

TABLE 4. Predicted performance (according to program FLIGHT) of male Bar-tailed Godwits initiating flight with given fuel stores and flight parameters (see Table 1) and flown until fat stores are depleted. Program FLIGHT assumes that a small part of the energy used comes from burning protein, primarily from pectoral muscle but also from other components of lean mass as well.

	At start of flight				At fat depletion				
Body drag coefficient	Body mass (g)	Lean mass (g)	Fat mass (g)	Pectoral muscle mass (g)	Body mass (g)	Pectoral muscle mass (g)	Distance covered (km)[a]	Days in the air	Air speed (m sec^{-1})
0.10	455	255	200	67	183	28	9303	7.0	15.3
0.10	485	285	200	72	213	32	8154	6.0	15.6
0.10	515	315	200	76	243	36	7240	5.3	15.9
0.05	455	255	200	67	188	30	12 883	8.2	18.2
0.05	485	285	200	72	214	33	11 308	7.0	18.6
0.05	515	315	200	76	244	37	10 049	6.1	19.0
0.05	485	285	200	54	213	24	11 308	7.0	18.6
0.05	515	285	230	76	202	29	12 928	7.9	19.0

[a] Distances covered based on flight at sea level.

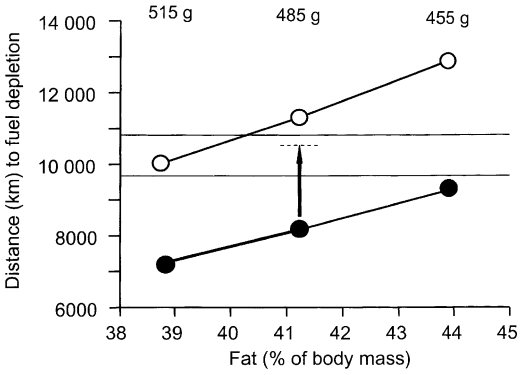


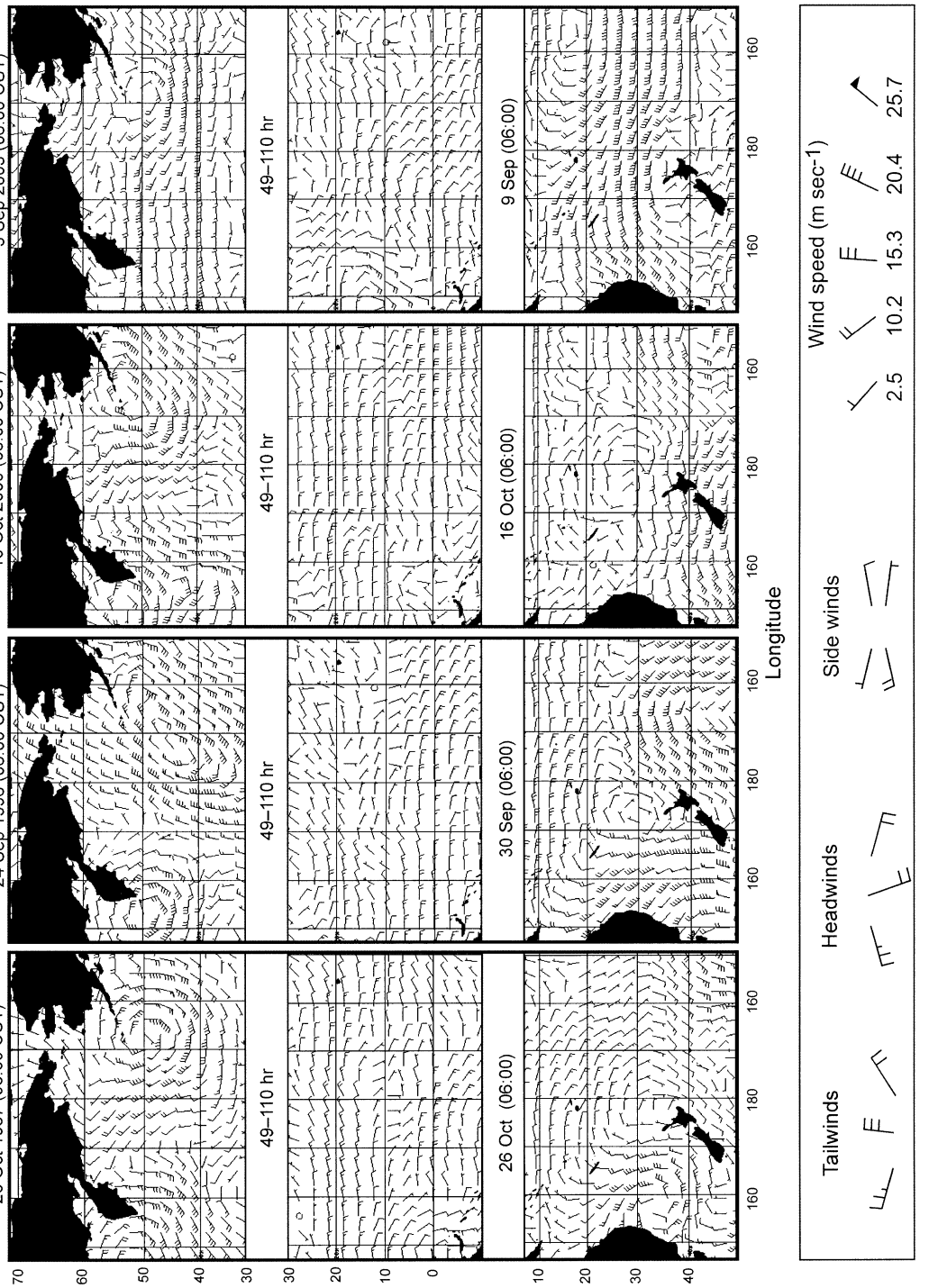
FIGURE 4. Predicted maximum flight range (the distance to fuel-depletion) in male Bar-tailed Godwits. Plot is a function of initial body mass (515, 485, or 455 g), variation in the percent fat of body mass at the start of the flight from Alaska (39–44%; with correlated variation in body mass, fat-free mass, and pectoral muscle mass, but with a constant fat load of 200 g), and two values for the body drag coefficient (BDC). Solid circles indicate simulations using a BDC value of 0.1, unfilled circles indicate simulations using a value of 0.05. The solid horizontal lines represent great circle distances transited by godwits: upper line at 10 800 km is distance between the northernmost staging site in Alaska (Yukon Delta) and the northern tip of the North Island, New Zealand; lower line at 9700 km is distance between southernmost staging site in Alaska (Nelson Lagoon) and Townsville, Queensland, Australia, the suspected northern portion of the nonbreeding range of *baueri* in Australia. For a bird with a starting body mass of 485 g, a BDC of 0.1, an average constant flight speed of 15.4 m sec^{-1}, but with an average tailwind of 4.5 m sec^{-1} for the entire distance, the flight range would be increased by 2000 km, as indicated by the arrow and broken horizontal line. Similar proportional increase in flight range would occur in birds having a BDC of 0.05 (unfilled circles).

ing northward migration (18.4 m sec^{-1}; M. Green and T. Piersma, unpubl. data), than for air speeds (15.6 m sec^{-1}) obtained with a body drag coefficient of 0.1 (Table 4).

Reducing body mass by 30 g and leaving fat mass at 200 g (44% fat) enhanced the predicted maximum flight range (Fig. 4), but led to inappropriately low arrival masses and very small pectoral muscle masses (Table 4). Increasing body mass by 30 g lean tissue (39% fat) led to lower maximum flight ranges but also to reasonable values for remaining body and pectoral muscle masses at the point of fat depletion (Table 4). When we decreased pectoral muscle mass at departure to 54 g based on the fraction of body mass measured in the sample of *baueri* from New Zealand (0.111; Battley and Piersma 2005), final body mass was of the right order but pectoral muscle mass (24 g) remaining after the flight was certainly too low (Table 4). When we gave birds with a lean mass of 285 g an extra 30 g of fat (thus increasing pectoral muscle mass from 72 g to 76 g), they increased their maximum flight range, but reduced final body mass and pectoral muscle mass to quite low values. Lastly, when we ''flew'' birds at 1500 m altitude instead of at sea level they increased their range by only 60–100 km but increased their optimal flight speed about 7%, resulting in a concomitant reduction in travel time (~9–12 hr).

DEPARTURES IN RELATION TO WEATHER

Actual departures of birds on southward migration from Alaska were observed on four occasions between 1987 and 2003 (Table 3). The


20 Oct 1987 (06:00 CUT)
24 Sep 1996 (06:00 CUT)
10 Oct 2000 (06:00 CUT)
3 Sep 2003 (06:00 CUT)
49–110 hr
26 Oct (06:00)
30 Sep (06:00)
16 Oct (06:00)
9 Sep (06:00)
Latitude
Longitude
Tailwinds
Headwinds
Side winds
Wind speed (m sec-1)
2.5
10.2
15.3
20.4
25.7

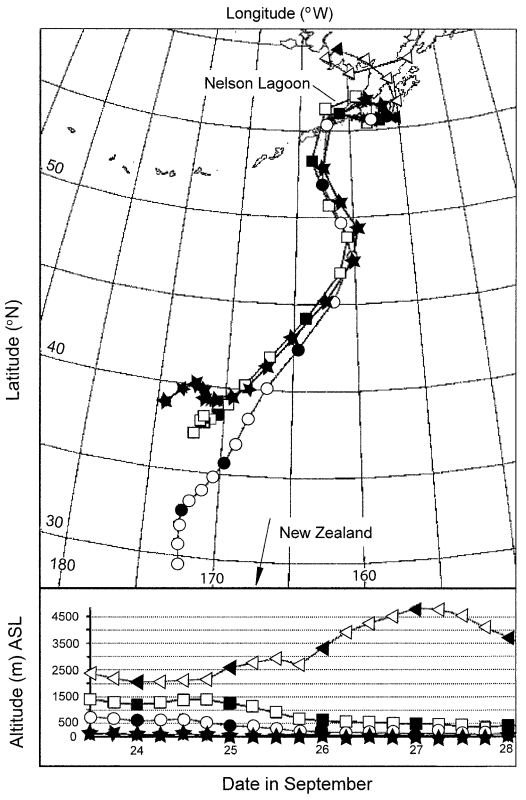


FIGURE 6. Air flow over a 5-day period for objects entering the air column at Nelson Lagoon, Alaska, at the time of the observed departure of godwits on 23 September 1996. The objects, entered into the air column at various altitudes, are then tracked at successive 6-hr intervals with filled star = surface, unfilled circle = 750 m, unfilled square = 1500 m, and unfilled triangle = 2500 m elevation above sea level (ASL). Their respective filled symbols denote 24-hr periods. During the initial 60 hr of the model run between Nelson Lagoon and about 40°N latitude, winds at the 750-m and 500-m altitude varied between 10–15 m sec^{-1}. The arrow to New Zealand approximates direction but not necessarily route taken.

1987 event entailed recovery of birds that died after colliding at night with a large radar dome near the distal end of the Alaska Peninsula (Piersma and Gill 1998); the three other departures were documented from on-ground observations (1996 and 2003) or from aerial surveys (2000). Observed departures spanned almost a 7-week period between early September and mid-October (Table 3).

All four events occurred in association with moderate troughs with imbedded storms having central pressures between 976 mb and 998 mb (average 984 mb) and centered between 650 km and 1400 km south of the departure sites (Table 3, Fig. 5). Such storms are propagated in the Aleutian low pressure system along a track that, beginning in September, passes south along the Aleutian Islands and then northward into the Gulf of Alaska. During the period 1976–2000, storms with central pressure of between 975 mb and 1000 mb occurred annually along this track on average twice in September, between two and three times in October, and just over three times in November. Local winds during the departure events varied in both direction and intensity, ranging between 0–10 m sec^{-1} from north to northeast. The positions of the storm centers at time of departure (Fig. 5) suggest birds would have to have flown on a slight west-southwest heading (200–240°) before obtaining maximum benefit from tailwinds, but once positioned within the 'upstream' side of the systems birds flying in a southerly direction would have encountered strong direct to quartering tailwinds averaging 15 m sec^{-1} (midpoint of ranges, Table 3). Winds of this approximate speed and direction would have been maintained on average over a distance of about 1000 km, with conditions associated with the 1996 departure, for example, extending almost 1500 km south (Table 3, Fig. 6).

Winds along the mid-portion (latitudes 20°N to 20°S) of each of the four suspected flight

←

FIGURE 5. En route winds (850 mb altitude = 1500 m) associated with the four recorded departures of godwits from Alaska. See Table 3 for location of departure sites. The upper panels represent winds at time of departure (±3 hr, CUT = Coordinated Universal Time), middle panels show typical conditions between the 49th and 110th hr of the flight, and lower panels show the conditions at the end of the projected 6-day transit time (but are also representative of the preceding 24–36 hr). Long, unflagged portion of the axis of each wind bar points towards direction wind is blowing; number and type of short flags perpendicular to long bar indicate wind speed. Original wind vectors were depicted in knots and converted here to m sec^{-1}. Legend indicates range of directions that would be tailwinds, headwinds, or side winds along proposed transpacific migratory corridor between Alaska and eastern Australia and New Zealand.

paths (Fig. 5) were very similar and characterized by light (2–8 m sec^{-1}) crosswinds or quartering winds. Once into the southern realm of the southeast trades and austral westerlies at about days five and six of the flight, godwits again experienced strong direct or quartering tailwinds over the last 1000 km of the flight, especially if New Zealand was the destination. Any birds attempting to go to eastern Australia during the 2003 event would have experienced moderate to strong headwinds from central Queensland south to Victoria, but mostly calm winds if landfall were in northern Queensland (Fig. 5).

DISCUSSION

The evidence we present supporting a direct nonstop flight by *baueri* godwits between Alaska and New Zealand is straightforward and compelling: (1) *baueri* godwits are extremely rare along the central East Asian mainland on southward migration, (2) peak southward departure from Alaska and peak arrival in New Zealand occur within the same relatively short period, and both are a month later than for godwits (*L. l. menzbieri*) that do follow a continental Asian route, (3) too few godwits have been noted in Oceania to suggest any regularly used intermediate stopover site(s), but the birds that are recorded there peak in occurrence and number in October and within a direct corridor linking Alaska and New Zealand/eastern Australia, especially near the terminus, where fallout of transients would be expected, (4) the annual occurrence of Hudsonian Godwits in New Zealand and eastern Australia—but their absence from mainland Asia—can best be explained by their accompanying Alaskan Bar-tailed Godwits on a transpacific flight, (5) birds appear energetically and mechanically capable of such a flight based on current knowledge of aerodynamics and measured fuel sources, and (6) known departures from Alaska coincide with favorable winds for a southward flight but are in opposition to a more southwesterly continental route. Aspects of several of these lines of evidence warrant additional discussion.

FACTORS CONSTRAINING FLIGHT RANGE

The simulations with program FLIGHT suggest that even under still air conditions Bar-tailed Godwits leaving Alaska staging sites with realistic body and fat mass values should be able to reach New Zealand in a nonstop flight of between 9800 and 10 700 km. If the godwits are able to routinely use tailwinds en route, we can relax the assumption of a body drag coefficient of 0.05 (but see Elliott et al. 2004) and accept a value closer to the more often used 0.1 (Kvist et al. 2001, Pennycuick and Battley 2003). In addition to fat as fuel, protein availability and water (dehydration) can limit flight range (Klaassen 1995, Jenni and Jenni-Eiermann 1999). For the *L. l. taymyrensis* subspecies during a 4300-km-long northward flight from western Africa to Europe, Landys et al. (2000) concluded that flights ranging in altitude from sea level to 3000 m would avoid dehydration, and in fact found no evidence for dehydration in arriving godwits. Interestingly, Landys et al. (2000) also had to assume a body drag coefficient as low as 0.05 for the virtual godwits to complete their flight.

Our simulations have made clear that the necessary minimum protein use during nonstop flights does limit maximum flight range. Birds leaving Alaska with a lean mass lower than 275 g are predicted to have exhausted their fat when their lean mass is as low as 200 g and their pectoral muscles have become tiny (Table 4). The small-sized juvenile Bar-tailed Godwits with a lean mass of only 166 g and a fat store of 200 g (Piersma and Gill 1998) are predicted to be able to cover more than 11 000 km nonstop. Not surprisingly, they are also predicted to arrive with perhaps unrealistically low lean and pectoral muscle masses (for a body drag coefficient of 0.05, lean mass after 11 000 km of flight under still air conditions would be 170 g and pectoral muscle mass 25 g; with a coefficient of 0.1 the predicted final mass values are 130 g and 20 g, respectively). Given such values upon arrival in New Zealand, it seems unwarranted to expect these birds to have been capable of reaching the South Pole, an additional distance of 6000 km, as predicted by Pennycuick and Battley (2003), who accommodated unrealistic lean mass values. Lowering the minimum energy obtained from protein to 2% does not resolve the problem. In view of the absence of hard body composition data for adult godwits, and the problematic departure condition of the juveniles from 1987, detailed studies examining departure body condition in relation to performance during the ensuing flight and pinpointing exact arrival time in New Zealand are clearly needed.

A DIRECT ROUTE OR ONE WITH STOPOVERS?

A direct flight by a congener. Hudsonian Godwits breed in subarctic and temperate North America and migrate to southern South America (Elphick and Klima 2002), yet are rare annual visitors to New Zealand (Higgins and Davies 1996, Elphick and Klima 2002) and occasionally elsewhere in Oceania (Watling 2001), with up to nine different individuals seen in a single year. It is highly unlikely that Hudsonian Godwits, though also long-distance migrants (McCaffery and Harwood 2000), reach southern Oceania by following a continental route via the East Asian mainland, a distance of over 16 000 km. Indeed, we could only find a single record of the species from Asia and that from Chukotka almost 150 years ago (in Kessel and Gibson 1978). It is also highly unlikely that birds reach New Zealand via a 9000-km-long flight across the Southern Ocean after an initial flight of 8000 to 11 000 km from eastern Canada to southern South America. The most logical explanation for their occurrence in New Zealand is that they accompany Bar-tailed Godwits on the godwits' southward flight across the Pacific (see also Kessel and Gibson 1978). Recent observations of small numbers of Hudsonian Godwits (all juveniles to date) among large flocks of Bar-tailed Godwits at principal Alaskan staging sites (R. Gill and B. McCaffery, unpubl. data) support this idea.

Stopovers. As it is energetically more favorable to cover a certain migration distance in many small steps than in one long hop (Piersma 1987), the assembled evidence that some 150 000 Bar-tailed Godwits annually make a 11 000-km-long nonstop flight from Alaska to New Zealand/eastern Australia begs the question of why do they not make stopovers, either along the East Asian mainland if such a route is followed or during a transpacific crossing. First, the evidence we have assembled fails to support use of a continental route, with or without use of stopover sites. Given the paucity of records of *baueri* along the East Asian mainland during southward migration, if they were migrating along the Asian coast it would entail a nonstop flight of almost 16 000 km, 40% longer than a flight directly across the Pacific. Such a long flight is improbable given the fuel loads of departing godwits and predicted arrival mass upon fuel depletion (contra Pennycuick and Battley 2003). In addition, during the recorded departure events, birds would have initially encountered moderate to strong headwinds and then a long fetch of strong southerly winds if they had followed a more southwesterly route along the Asian mainland. Such a flight would have forced birds to either fly into opposing winds or detour around the systems, both of which would have added substantially to energetic costs.

We likewise found no evidence suggesting use of intermediate stopover sites if birds followed a direct route across the Pacific. Arguably, the Pacific Ocean is vast and it could harbor yet undiscovered stopover site(s), but the region has received considerable attention from ornithologists, and its indigenous peoples are intimately in tune with their natural resources. We find it beyond reason to expect the annual use by 150 000 godwits at stopover site(s) in Oceania to have gone undetected by either group of people. Indeed, the 80-year span of records we searched accounted for a total of only about 4000 godwits having been recorded throughout all of Oceania—this from a projected total of some 12 million godwits that could have stopped somewhere en route during this period. And though we cannot rule out that birds alight on open ocean waters during transit, it likely would be for relatively short periods and then related to adverse conditions (Piersma et al. 2002) and not for rest.

Thus, a single flight over the Pacific is not only likely but in several ways advantageous: it may be safer (there are rarely aerial predators in central Oceania; cf. Ydenberg et al. 2002), healthier (as encounters with pathogens will be avoided; Piersma 1997), and faster and more direct (as the time to settle at new stopover areas is avoided; Alerstam and Lindström 1990). It could also indicate the high quality of the western Alaskan staging sites relative to potential staging/stopover areas along the East Asian coastline or throughout Oceania (Gill and Handel 1990, Gudmundsson et al. 1991). Indeed, soft substrate intertidal habitat, the preferred feeding substrate for nonbreeding godwits, is extremely limited throughout Oceania, occurring mostly on Fiji, the one site in Oceania that regularly hosts godwits (Watling 2001).

Our story has its perplexities. There are three reports of putative *baueri* from the East Asian mainland during the southward migration period—one of a Victoria, Australia-flagged bird seen in the North China Sea region in late August, and two of New Zealand-banded birds

from Kamchatka, Russia; one seen in mid-August and another shot in early October (Riegen 1999, Gosbell 2004, J. Wilson and C. Minton, unpubl. data). One or more scenarios likely explain these three exceptions to an otherwise clear pattern of subspecies segregation during southward migration. First, though the two subspecies are largely segregated on the nonbreeding grounds, there are records of each occurring in the other's range (J. Wilson and C. Minton, unpubl. data) and thus potentially occurring elsewhere outside normal distributions. A confounding factor is the uncertain taxonomic status (Engelmoer and Roselaar 1998, Tomkovich and Serra 1999) and unknown nonbreeding range of the small population of godwits that nests in the Anadyr Lowlands and southern Chukotks Peninsula, Russia, intermediate between the ranges of *menzbieri* in Siberia and *baueri* in Alaska (McCaffery and Gill 2001). Phenotypic differences are slight, with Anadyr birds more closely resembling *baueri* in both size and plumage than they do *menzbieri* and thus more likely to be identified as *baueri* during banding. The recovery of the New Zealand-banded bird in southern Kamchatka, Russia, in October is a bit more difficult to explain, especially since most godwits have departed estuaries along the west coast of Kamchatka by early September (Gerasimov and Gerasimov 1998). If the Anadyr population proves distinct, it is likely the source of birds reported in Japan in September and in Micronesia where, though few in number, specimens of putative *baueri* have been recorded during southward migration (Stickney 1943, Baker 1951, Stinson et al. 1997), considerably west of a direct migration corridor between Alaska and New Zealand or eastern Australia. The occurrence of godwits in Micronesia is likely explained by fallout of migrants coming from the Sea of Okhotsk and Japan to northern Australia along a direct route that passes over the Northern Mariana archipelago. A radar study of shorebird migration over Guam during mid-August to late October showed just such a pattern (Williams and Williams 1988, 1999).

THE ROLE OF WIND SYSTEMS OVER THE PACIFIC

The *baueri* subspecies of Bar-tailed Godwit can be added to a growing list of birds that have evolved wind-sensitive migration strategies—especially during southward migrations—within the subpolar marine low pressure belt that circles the northern hemisphere (Richardson 1979, 1990, Åkesson and Hedenström 2000, Green 2003, M. Green and T. Piersma, unpubl. data). This phenomenon is especially evident in the North Pacific, where the Aleutian low pressure system shapes and dominates weather and wind patterns throughout the year (Christoforou and Hameed 1997, Overland et al. 1997). In particular, two taxa of large-bodied, medium-distance migrant geese annually initiate transoceanic flights from the Alaska Peninsula to the Pacific Coast of North America in conjunction with the passage of moderate to strong low pressure systems (Dau 1992, Gill et al. 1997). Not surprisingly, even small-bodied birds such as Dunlin (*C. alpina*) having similar nonbreeding ranges, often depart on the same weather systems as used by geese (Warnock and Gill 1996, R. Gill, unpubl. data). The emerging pattern is that godwits, geese, and Dunlin can use the same storms, only varying their departures in accordance with the position of the storm center and the birds' final destination.

Evolving a migration system in conjunction with winds at the departure site is one thing but, in the case of godwits that are transiting the entire Pacific, they must pass through at least five other latitudinal zones of defined winds and pressure. It is beyond the scope of this paper to present a thorough analysis of wind conditions along the entire projected flight path (cf. Piersma and Jukema 1990, Piersma and van de Sant 1992, Åkesson and Hedenström 2000). But what emerges from the four cases we studied suggests that winds were generally favorable throughout the migration corridor during the calculated 6-day transit time and certainly in no instance was there strong opposing wind for any appreciable distance. The most obvious question relating to this is to what extent local departure cues are related to favorable 'downstream' winds? Is weather across the Pacific teleconnected such that certain departure cues at northern latitudes assure relatively favorable conditions along most of the route (McCaffery and Gill 2001)? The Aleutian low pressure center is a large-scale dominating feature of the North Pacific (Christoforou and Hameed 1997, Overland et al. 1997) that has obviously shaped the evolution of equally large-scale geographical migration patterns, similar to systems described elsewhere in the northern hemisphere (citations in Green

2003). But the godwits' migration strategy, involving flights that span two hemispheres, was likely not selected for based solely on factors occurring over just a portion of the range and independent of those elsewhere along the migration corridor.

This raises obvious questions about global climate change and its effects on wind regimes and thus on wind-selected avian migrants. The ecological effects of climate fluctuations are many and projected to be most profound in regions with large-scale patterns of climate variability such as the North Atlantic and North Pacific (e.g., Stenseth et al. 2002). Global climate change models suggest an intensification of propagating weather systems moving across the North Pacific. Such would result in a shift of the Aleutian low center eastward that would in turn increase the number and intensity of storms and bring stronger northerly winds over a longer fetch on the backside of individual low pressure centers. Godwits may, however, be able to adapt to this as the Aleutian Low and adjacent Hawaiian High have been found to shift position and intensity (seesaw pattern) on a decadal scale during most of the twentieth century (Christoforou and Hameed 1997, Overland et al. 1997). The phenomenon, however, also needs to be assessed in the southern hemisphere in terms of teleconnection between the two hemispheres.

Development of suitable remote sensing satellite technology would greatly enhance our understanding of the complexity of the godwits' migration system and flight behaviors of long-distance transoceanic migrants in general. With such technology, answers would be forthcoming to questions about (1) mechanisms of orientation, (2) how birds select winds (vertical and lateral) at all stages of the flight, (3) whether and how they compensate for wind drift, (4) whether they adjust airspeed during the course of the flight, and (5) the extent to which they can assess and react to changes in downstream flight conditions.

THE PACIFIC AS AN ECOLOGICAL BARRIER?

Although the Pacific may be an ecological barrier for humans and for numerous Palearctic and Nearctic migratory landbirds (Baker 1951, Pratt et al. 1987), it does not appear to be a barrier for the *baueri* race of the Bar-tailed Godwit, at least under the observed ecological conditions associated with departures from Alaska and arrivals in New Zealand and eastern Australia. The Pacific as a barrier is further mollified considering that southward migration by godwits appears to be wind-selected, at least at departure, and that such winds appear to confer significant energy savings. With inferred high rates of annual survival (A. Riegen in McCaffery and Gill 2001, R. Gill, unpubl. data), experienced adults may actually encounter few losses during their southward journeys, but it is quite possible that the situation is different for juveniles migrating their first time, especially if they fly in flocks composed only of inexperienced juveniles. And such appears to be the case, at least concerning late-departing birds from Alaska and late arrivals in New Zealand (Piersma and Gill 1999, Riegen 1999, R. Gill, unpubl. data). The age structure of the population occurring during the nonbreeding season in Fiji is poorly known (D. Watling, pers. comm.), but one could expect a high proportion of inexperienced juveniles to occur there since Fiji is the last suitable land before a 2000-km-long open-ocean crossing to New Zealand.

Future studies should focus primarily on questions related to flight behaviors throughout the migration corridor, but equally rewarding would be to learn both local and regional patterns of arrival and subsequent movements of birds. For example, is the movement of godwits from Queensland, Australia, to New Zealand (Riegen 1999) an annual event and are these mostly juveniles that are incapable of the longer direct flight to New Zealand?

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